DIVERSE FOSSIL EPACRIDS (STYPHELIOIDEAE; ERICACEAE) FROM EARLY PLEISTOCENE SEDIMENTS AT STONY CREEK BASIN, VICTORIA, AUSTRALIA

Gregory J. Jordan[1], Kate E. Bromfield[1,2], J. M. Kale Sniderman[3], Darren Crayn[4]

[1] School of Plant Science, University of Tasmania, Private Bag 55, Hobart, Tas., 7001, Australia. [2] Current address: Centre for Marine Studies, University of Queensland, Brisbane, Queensland 4072, Australia. [3] School of Geography and Environmental Science, Building 11, Monash University, Vic., 3800, Australia. [4] National Herbarium of New South Wales, Botanic Gardens Trust, Mrs Macquaries Rd, Sydney 2000, Australia

[1] Author for correspondence; e-mail greg.jordan@utas.edu.au

Keywords: Epacrid, Styphelioideae, evolutionary radiation, Quaternary, fossils, Australia, sclerophylly, scleromorphy

Short Title: Jordan et al. - Diverse Early Pleistocene epacrids

Abstract

There is intense current interest in the radiation of the scleromorphic groups that dominate the Australian flora, but at present, only Proteaceae and Casuarinaceae have fossil records detailed enough to provide useful evidence of the timing of these radiations. This paper records a diverse assemblage of fossil leaves of another major scleromorphic group, the epacrids (subfamily Styphelioideae of Ericaceae, formerly known as Epacridaceae). The fossils are from Stony Creek Basin, in the western uplands of Victoria, Australia, and are of earliest Pleistocene age (circa 1.6 million years old). They include 19 forms sufficiently distinct to constitute different species. This diversity is considerably greater than the extant diversity of epacrids in the region. Published taphonomic data are used to argue that the actual diversity of the source vegetation of the fossil flora may have been significantly greater and comparable to the current local species richness of the centres of diversity. Ten of the fossil species are assigned to the largest extant tribe (Styphelieae), eight are assigned to Epacrideae and one is assigned to Cosmelieae. This evidence is used to argue that substantial radiation of the epacrids had occurred by the beginning of the Pleistocene.

Introduction

The timing of the radiation of the scleromorphic flora has long been one of the central questions in the history of Australian vegetation (e.g. Crisp et al. 2004). Since scleromorphs (hard-leaved, mostly slow growing species) can be considered as an extreme in a continuum of ecological strategies, it is not possible to make an absolute distinction between scleromorphs and non-scleromorphs. However, Australia's flora has long been recognised as being strongly biased towards the scleromorphic end of this continuum, with many unambiguous scleromorphs in Proteaceae, Ericaceae, Casuarinaceae, Fabaceae, Myrtaceae and other families. A high proportion of this diversity occurs in seasonally dry areas, especially south-western Australia. However, scleromorphy is also prominent in some distinctly wet habitats, and most researchers would consider that nutrient-poor soils have played as great a role in the evolution of scleromorphs as dry climates (e.g. Hill 1998).

Scleromorphy is ancient, at least in the families Proteaceae and Casuarinaceae, as shown by scleromorphic fossils of Late Paleocene age (Carpenter *et al.* 1994; Scriven and Hill 1995). Scleromorphic Fabaceae and Ericaceae subfamily Styphelioideae (Carpenter 1991; Jordan and Hill 1995) and diverse scleromorphic Proteaceae (Jordan *et al.* 1998) were present by the Early Oligocene. However, apart from some species of *Banksia* s.l., none of these Paleogene Proteaceae can be assigned to any of the genera (e.g. *Grevillea/Hakea*, *Persoonia* and any of the diverse genera in Proteoideae) that are diverse in the modern scleromorphic flora. Thus, it is plausible that many of the products of the early radiation of scleromorphs represent extinct lineages. Hill (1994, 1998) argued that, although scleromorphy evolved early in Proteaceae and Casuarinaceae, physiological adaptations to dry climates first appear in the fossil record in the Miocene. This conforms well to other evidence suggesting drying of climates in southern Australia (see evidence presented by Frakes 1999).

Therefore, although scleromorphy is an ancient syndrome in Proteaceae, Casuarinaceae, Ericaceae, Fabaceae and perhaps Myrtaceae, it remains possible that most of the diversification of these taxa is recent. Thus, there is evidence suggesting recent and very rapid radiation of dry climate taxa in South Africa (Klak et al. 2004). This ambiguity is expressed by Hopper and Gioia (2005), who argued that much of the massive radiation of scleromorphs in south-western Australia probably occurred in response to the rapid climate cycles of the Pleistocene, but that the scleromorphic flora also included much older components. Molecular clock-type approaches show "broomstick" evolution in several groups suggesting relatively recent radiation (e.g. Crisp et al. 2004), although these approaches are still limited by a scarcity of calibration points.

The Ericaceae form significant components of the scleromorphic floras of south-western and eastern Australia. Almost all species are in the distinctive subfamily Styphelioideae (commonly known as epacrids and formerly recognised as the family Epacridaceae). This monophyletic group (Crayn *et al.* 1998; Kron *et al.* 2002) is mainly Australian, although species also occur in the Pacific (most notably New Zealand, New Caledonia and Hawaii) and Malesia, and one species occurs in temperate South America. Like many other Ericaceae, the Styphelioideae are generally associated with nutrient-poor, often acidic soils. Virtually all species of Styphelioideae are scleromorphic. Most have very small leaves, usually less than $1cm^2$ in area. The notable exceptions are a few species of *Dracophyllum* and *Richea* with leaves more than 0.5 m long, although a few species of other genera (e.g. *Leucopogon*, *Cyathodes* and *Cyathopsis*) can have leaves over 5 cm long. Although not formally documented, the leaves of most species are quite hard due to the presence of lignified epidermis and fibre bundles associated with the veins (Stevens *et al.* 2004), and many are pungent.

The Styphelioideae contain more than 450 species in 37 genera and seven tribes (Stevens et al. 2004; Quinn et al. 2005). This species richness is unevenly distributed

phylogenetically, and suggests extensive radiation in tribe Styphelieae, especially in at least two clades in the paraphyletic genus *Leucopogon* (Styphelieae) (Taafe et al. 2001), and lesser radiations (and/or greater extinctions) in Richeeae, Cosmelieae and Epacrideae (Fig. 1).

Three main centres of diversity (south-western Western Australia, Tasmania and central eastern New South Wales; Fig. 2) contain over 75 % of the species and all but four (*Agiortia*, *Cyathopsis, Decatoca* and *Lebetanthus*) of the genera. These regions have disparate climates, but are characterised by nutrient poor soils (often extremely so). The greatest species richness is in south-western Australia, with approximately 190 named species in 17 genera (Keighery 1996, 2002; Crayn *et al*. 2003, 2005; Cranfield 1998; 2002), and many undescribed taxa (see http://florabase.calm.wa.gov.au/). The region is characterised by a Mediterranean-type climate, with warm to hot, dry summers and cool, wetter winters and a range of soils, often formed on deep sands, laterites or granites, although almost all are very nutrient poor (Hopper and Gioia 2004). Tasmania is the second centre of diversity (92 species, 19 genera – Buchanan 2005; Quinn *et al*. 2005). Within Tasmania, the wet forest and montane floras of the centre and west contain arguably the highest phylogenetic diversity in Styphelioideae, with six of the seven tribes represented in this small region, whereas Western Australia contains five and New South Wales four (Crayn *et al*. 1998). Western Tasmania is characterised by cool, wet climates and peaty soils overlying quartzite and other highly silica-rich rocks (Jackson 1999). Relatively high diversity (~63 species in 15 genera; Powell 1992; Cherry *et al*. 2001) also occurs in central eastern New South Wales (near Sydney), particularly on soils derived from Hawkesbury sandstone. This region has moderately high rainfall year round and the Hawkesbury sandstone soils are nutrient poor. New Zealand is a minor centre of diversity with c. 48 species, mostly in the genus *Dracophyllum* (de Lange *et al*. 2006).

Considering the general factors that affect the incidence of plant organs in the fossil record, Styphelioideae would appear to be good candidates for fossilisation. These factors include the distance of source plants from a site of fossilisation (usually a wet place), the abundance of organs on the source plants, the resistance of these organs to decay, the presence of distinctive features on these organs to allow their identification, and the availability of palaeobotanical expertise. Many species of Styphelioideae occur in wet habitats. The toughness of the leaves, and perhaps the small leaf size (resulting in high numbers of leaves being available for fossilisation) should favour fossilisation. Hill and Gibson (1986) showed that leaves of a number of species of Styphelioideae were well represented in the superficial sediments of the floor of a subalpine lake in Tasmania. Also, the leaves and fruit have distinctive features that should allow fossils to be readily recognised (Jordan and Hill 1995). Several major groups can be recognised, and closely related species can have quite different leaf form. However, it can be difficult to differentiate among related genera, and assigning fossil leaves to living species is rarely possible (Jordan and Hill 1995). The endocarps of one tribe, Styphelieae, are distinctive.

In spite of their apparent potential for fossilisation, the Styphelioideae have a sparse fossil record (Jordan and Hill 1995; 1996). Fossil pollen shows that the Ericaceae was present in Australia in the Late Cretaceous (Dettmann 1994). However, since this pollen is broadly consistent with a wide range of Ericaceae, there is no unambiguous evidence for the presence of the Styphelioideae before the Early Oligocene (Jordan and Hill 1996). The Oligocene fossils are small, scleromorphic leaves of tribe Richeeae and either tribe Archerieae or Epacrideae (Jordan and Hill 1995; 1996). However, these fossils say little about radiation within Styphelioideae because they represent only a few species, none of which are from derived taxa that would indicate high levels of differentiation within the subfamily (Jordan and Hill 1995; 1996). Much younger (Early Pleistocene) fossils show the presence of a

slightly wider range of species in Tasmania, but do not demonstrate the presence of high diversity (Jordan and Hill 1996).

The timing and location of diversification of the Styphelioideae therefore remains unclear. The widespread distribution of the family within Australasia with a number of wide disjunctions, combined with high levels of endemism (~98% species endemism in Western Australia [Keighery 1996], and 64% species endemism in Tasmania [Buchanan 2005]) could be used to argue for antiquity of this radiation. However, this argument assumes some uniformity of rates of evolution. It also assumes a low frequency of long-distance dispersals, whereas some distributions of Styphelioideae suggest that this may not be the case. Thus, *Leucopogon parviflorus* (Andrews) Lindley and *Sprengelia incarnata* Smith occur naturally in both Australia and New Zealand and species of *Leptecophylla* are found on several oceanic islands, including Hawaii (Weiller 1999), distributions which are extremely difficult to explain except as long distance dispersal events (Jordan 2001). *Cyathodes dealbata* R.Br. (Tasmania) and *C. pumila* Hook. f. (New Zealand) may be conspecific (Quinn *et al*. 2005) and therefore fall into the same category. *Leptecophylla* [*Cyathodes*] *juniperina* (Forst. & G.Forst.) C.M.Weiller subsp. *juniperina* and *Pentachondra pumila* (Forst. & G.Forst.) R.Br. also occur in both Australia and New Zealand, although molecular analyses reveal considerable differences between the Australian and New Zealand populations of each species (Quinn *et al*. 2005; C.J. Quinn, M.M. Heslewood and D.M. Crayn, unpublished data).

This paper uses fossil evidence from well-preserved macrofossil material from Stony Creek Basin, Victoria, Australia, to investigate diversity of this group in the earliest Pleistocene, and discusses the question of whether the diversity of Styphelioideae is essentially a product of the climatic cycles of the Pleistocene. The site contains a very diverse array of fossil plant and insect parts, including conifers, ferns and a wide range of angiosperms. This paper describes only the epacrids from this assemblage.

Materials and Methods

The fossil site

The fossils described here were extracted from Stony Creek Basin, in the western uplands of Victoria, Australia (144.13ºE, 37.35ºS, 550 metres above sea level; Fig. 2). The Basin is a small paleolake deposit of probable maar origin. The total drainage catchment of the basin at present is approximately 0.5 km^2 and may have been slightly smaller at the time of deposition of the fossiliferous sediments. The lake sediments comprise ~40 m of black, organic-rich, silty clays.

The age of the basin is described in detail by Sniderman et al. (2007). In brief, zircons from a core extracted by hollow augur drilling in 2000 give ages of 1.93 ± 0.18 million years (Ma) for a thin volcanogenic layer at 29 m depth and 1.99 ±0.43 Ma for fine sands at the base of the core. These can be used to indicate that the sediments are no older than the latest Pliocene. The sediments in the upper 25 m of the core are of reversed magnetic polarity, and therefore predate the Brunhes/Matuyama polarity transition at 0.78 Ma, while below 25m are of normal polarity (Sniderman et al. 2007). Considering the zircon dates, this transition can be attributed to end of the Olduvai subchron (1.781 Ma; Lisiecki and Raymo 2005). Correlation of the pollen record with the astronomical timescale based on an age model derived from counting annual sediment laminae indicates that deposition of the pollen sequence occurred between 1.83-1.55 Ma (Sniderman et al. 2007), which straddles the Pliocene-Pleistocene boundary at 1.81 Ma (Gradstein et al. 2004).

The fossils described here were extracted from two independent samplings from the site. Some fossils were extracted from two portions of the core described by Sniderman et al. (2007). These parts were between 2.6 and 4.35m depth and between 19.6 and 22.1m depth, which correspond to approximately 1.6 and 1.7 Ma, respectively. However, most fossils were

extracted from a sampling from the wall of a large pit in the basin dug with an excavator in February 2002, approximately 15 m from the core hole. Material was collected from an exposed, undamaged wall of this pit from a depth of 4-6m. Palynological analyses suggest this material is of equivalent age to the 2.6-4.35 m core samples (i.e. ~ 1.6 Ma).

Fossil extraction and analysis

From the pit, fossils were extracted from blocks of sediment of approximately 500 cm^3 sampled at 10 cm intervals. From the core, fossils were extracted from samples of approximately 500 cm^3, representing 20 cm intervals down the core. Fossils were extracted by soaking the sediment samples in a concentrated (~ 5%) aqueous solution of tetrasodium pyrophosphate until the sediment disaggregated (usually taking about 3 weeks), followed by sieving through nested 850μm and 160μm sieves. The 850μm sievings were sorted under a binocular microscope at 8-12x magnification, and all identifiable plant fragments removed manually. No additional identifiable plant fragments were found in scans of subsamples of the 160μm sievings.

The macrofossils were found in two states of preservation. Some showed plastic organic preservation, with excellent preservation of cuticles, but without recognisable internal anatomy. Other fragments were carbonised. These specimens were brittle, but often showed good to exceptional preservation of microscopic surface features and internal anatomy. In particular the outlines of the epidermal cells were often apparent on the leaf surface or were exposed by erosion of the leaf surface, and cells of the mesophyll and vascular tissue could sometimes be observed after breaking the fossils. It is not clear whether the carbonisation was the result of burning or of diagenetic processes in the sediments. However, a few specimens showed intermediate states of preservation, with carbonised inner parts, but organically preserved cuticles, implying that at least some of the carbonised specimens had not been burnt. The fossils were often small in comparison to comparable organs of related living species. This could be in part due to diagenetic shrinkage. However, there was little or no indication of distortion of cell shapes by any such process. Also, there was no indication of differences in size between fully carbonised specimens and specimens of the same species showing plastic organic preservation. It therefore appears unlikely that there was a large degree of shrinkage.

Whole fossils were mounted on aluminium stubs, sputter coated with gold or platinum to a thickness of approximately 20 nm, then observed under high vacuum with either an Electroscan ESEM or a FEI Quanta 200 ESEM operating at 15 kV. When possible, individual specimens were inverted after observation or broken and set on edge, recoated, then observed again under the same conditions.

Fossil identification

Jordan and Hill (1995) described two genera for fossil leaves of Styphelioideae with preservation of cuticular anatomy. These genera were *Richeaphyllum*, used for species of Richeeae, and *Epacriphyllum*, used for other Styphelioideae except Prionoteae and Cosmelieae. Jordan and Hill (1995) also described some key features useful in identifying fossil leaves of Styphelioideae (see Fig. 3).

Epacriphyllum was characterised by (1) hypostomatic leaves that possess entire margins or margins with fine serrations that are not associated with veins (Fig. 3A-F), (2) more-or-less rectangular epidermal cells aligned parallel to the main veins, and with sinuous to strongly sinuous anticlinal walls (Fig. 3G); (3) stomata aligned parallel to the main veins (Fig. 3G); and (4) venation that is parallel or sub-parallel (except in Prionoteae and some species with very narrow leaves and only one main vein). In addition, many members of Styphelieae have (5) very short, unicellular conical trichomes which cover the stomatiferous parts of the leaf (Fig. 3H-I).

Richeaphyllum has features 1-4 (although a few species have a few stomata on the adaxial surface), and two additional features (6) sessile leaves tapering evenly from sheathing leaf bases and (7) paracytic stomata. Leaves of Cosmelieae (Fig. 3C) are similar to Richeeae except that they have cyclocytic stomata and are amphistomatic.

The good preservation of many of the Stony Creek Basin fossils allows the observation of significant anatomic features not considered by Jordan and Hill (1995). The location of vascular bundles is perhaps the most significant of these taxonomically. In species of Archerieae, Epacrideae, Oligarrhenae and Cosmelieae, the vascular bundles are separated from the abaxial epidermal cells by mesophyll cells (Watson 1967; Quinn et al. 2005. In many Richeeae the vascular bundles are connected to both adaxial and abaxial epidermides by multiple layers of fibres. In most Styphelieae the fibre bundle abaxial to each vascular bundle is attached directly to the abaxial epidermis, but in others the fibre bundles are separated from the abaxial epidermis either by a single layer of small lightly lignified cells, or by a continuous or discontinuous layer of small unlignified cells, or in two genera by one or more layers of mesophyll tissue (Watson 1967; Quinn et al. 2005; C. J. Quinn pers. comm.). In addition, the mesophyll of Australian *Archeria* species is detached from the abaxial epidermis. Prionoteae have more typical dicot leaves with secondary veins leading to teeth.

Systematics

Family-Ericaceae

Subfamily-Styphelioideae

Tribe-Epacrideae or Archerieae

Epacriphyllum sp. 1 (Fig. 4)

Specimens examined. SCB190_o_epac1, SCB170_o_epac12

Description. Leaves hypostomatic, broadly cordate, about 0.7mm long, 1mm wide, slightly concave above, apparently glabrous, margins thick, entire, apex acute but not mucronate. Veins palmate with occasional secondary branches diverging at a very low angle from the main veins, not raised above the lamina. Petiole about 0.1mm long, 0.2mm wide, flexed towards the abaxial surface by approximately 90˚. Epidermal cells rectangular, with sinuous walls, 20-25µm long, 12-20µm wide, those of the midrib region aligned with the midrib, those of the upper and mid lamina diverging at an angle of approximately 30º, those towards the base diverging at higher angles, those in the basal lobes parallel to the leaf margin. Stomata aligned more or less parallel to the epidermal cells. Outline of guard cell pairs circular, 18-21µm long.

Comments. These tiny leaves are consistent with Epacrideae or Archerieae, with more or less rectangular, sinuous epidermal cells; stomata aligned parallel to these cells; and leaf form similar to many Epacrideae (e.g. *E. microphylla*; Fig. 3E). The leaves are, however, unusual for Styphelioideae in that the epidermal cells and stomata are not parallel to the midrib. However, the arrangement of stomata and epidermal cells of *E. microphylla* is similar to that of the fossils. *Epacris microphylla* differs from the fossils in being narrower and having a pungent apex. Several species of *Epacris* (e.g. *Epacris navicularis* Jarman, *E. petrophila* Hook.f. and, occasionally, *E. microphylla*) have leaves of similar size, at least in some populations.

Epacriphyllum sp. 2 (Fig. 5)

Specimens examined. SCB170_o_epac9

Description. Leaves hypostomatic, linear, narrow elliptical in cross-section, at least 4.5mm long (apparently at least 8mm long), approximately 0.75mm wide, with a short broad petiole (0.3mm wide, ~ 0.4mm long), reflexed at an angle of almost 90˚. Epidermis one cell thick, cells linear, ~15µm wide, up to 45-60 µm long, ~12µm tall, with acute ends. Stomata

arranged more or less uniformly on each side of the midrib, aligned parallel to the midrib, outline of pair of guard cells elliptical, 20-25µm long, 13-17µm wide. Vascular bundles 70-100µm wide, placed approximately mid-way between the adaxial and abaxial surfaces. Three vascular bundles of approximately similar size present about 1.5 mm above the leaf base. Palisade mesophyll 1 layer thick, cells ~40µm tall, 15-20µm wide, spongy mesophyll well developed, occupying approximately 2/3 of the thickness of the leaf, attached to the lower epidermis.

Comments. This fossil is consistent in all features with Epacrideae or Archerieae. Although these leaves are very similar in size and shape to *Epacriphyllum* sp. 11 (see below), they differ greatly in anatomy. The sinuous epidermal cells are obvious in surface view, less elongate than in *Epacriphyllum* sp. 11, and the cross sectional anatomy is quite distinct – with the epidermis only one cell thick and the vascular bundles placed midleaf (rather than adjacent to the abaxial epidermis).

Epacriphyllum sp. 3 (Fig. 6)

Specimens examined: SCB1985_epac2; SCB90_o_epac3

Description. Leaves hypostomatic, linear, distinctly thick (elliptical) in cross-section, 0.5 to 0.7 mm wide, 4-5 mm long. Petiole 0.2-0.3mm wide, ~ 0.4 mm long, straight. Apex obtuse. Abaxial epidermal cells 15-17µm wide; 30-35µm long sinuous walled, square ended. Stomata arranged more or less uniformly in one band on each side of the midrib, guard cells aligned parallel to the midrib, outline of pair of guard cells circular or wider than long, 15-17µm long, 16-18µm wide. Adaxial epidermal cells similar to abaxial epidermal cells.

Comments. This species is similar to *Epacriphyllum* sp. 2, but differs in the size and shape of the petiole – the petiole in this species is much narrower, and more elongated and is not bent. Furthermore, the epidermal cells differ in being square ended and shorter than in *Epacriphyllum* sp. 2. The stomata are not elongated, as in *Epacriphyllum* sp. 2.

Epacriphyllum sp. 4 (Fig. 7)

Specimens examined. SCB170_epacris1

Description. Leaves hypostomatic, broadly ovate/ovate triangular, widest immediately above the base, ~ 4mm long, 2.5mm wide, thick (~400µm), slightly concave above, apparently glabrous, margins thick, entire, apex acute, mucronate (presumably pungent). Petiole about 0.4mm long, 0.5mm wide, flexed towards the abaxial surface by approximately 90˚. Epidermal cells rectangular, with sinuous walls, ~25-30µm long, ~15µm wide. Stomata aligned more or less parallel to the epidermal cells. Outline of guard cell pairs circular, 23-25µm long. Palisade mesophyll cells in two layers, ~60µm long, ~10µm wide. Vascular bundles near to the abaxial leaf surface, but separated by a single layer of parenchyma cells.

Comments. This species is represented by one specimen that is clearly distinct from the other species described here. It is much larger than *Epacriphyllum* sp. 1, has a mucronate/pungent apex and larger stomata. It also has much larger stomata than *Epacriphyllum* sp. 5 (~25µm long *versus* ~13µm long), and has narrower palisade mesophyll cells (~10 µm wide *versus* ~ 18 µm wide). This species is generally consistent with Epacrideae, but the vascular bundles close to the abaxial mesophyll are more typical of Styphelieae.

Epacriphyllum sp. 5 (Fig 8)

Specimens examined. SCB170_o_Epac4, SCB Toupac2, SCB180_o_Epac3, SCB180_epac20, SCB190_o_Epacris1; SCB190_epac2, SCB200_o_Epac1, SCB1985_epac

Description. Leaves hypostomatic, ovate elliptical, 2-2.5 mm long, 1-1.5 mm wide, flat to slightly concave above, apparently glabrous, margins thick, entire, apex acute, not mucronate. Venation palmate/subparallel with ~7 veins. Petiole ~0.2-0.3 mm long, ~ 0.3 mm

wide, bent at an angle of approximately 45˚ towards the abaxial surface. Abaxial epidermal cells sinuous walled, 35-45µm long, ~18µm wide. Stomata aligned more or less parallel to the epidermal cells. Outline of guard cell pairs circular, 15-18µm long. Adaxial epidermal cells 25-35µm long, 10-13µm wide, ~10µm thick. Palisade mesophyll cells in two layers, ~50µm long, ~18µm wide. Vascular bundles placed just less than half way between the abaxial and adaxial leaf surfaces.

Comments, This is a reasonably common species, and is entirely consistent in all features with a number of species of *Epacris*, such as *E. heteronema* Labill. Differences from *Epacriphyllum* sp. 4 are noted in the comments on that species. It is much larger than and different in shape from *Epacriphyllum* sp. 1. This species is similar to some previously published fossils of Styphelioideae. The Early Oligocene species from Tasmania, *Epacriphyllum macphailii* G. J. Jord. & R. S. Hill, has similar leaf shape and similar sized stomata, but larger leaves (Jordan and Hill 1995). It is also similar to Early Pleistocene species from Tasmania (Jordan and Hill 1996).

Epacriphyllum sp. 6 (Fig. 9)

Specimens examined. SCB180_o_Epac4, SCB200_tiny_Epac

Description. Leaves hypostomatic, ovate-lanceolate, tapering more or less uniformly from approximately ¼ of the way up the leaf, 2-4 mm long, ~0.8 mm wide, slightly concave above, apparently glabrous, margins thick, entire, apex acute, not mucronate. Leaf subsessile, petiole flat, ~0.1 mm long, 0.2-0.3 mm wide. Abaxial epidermal cells elongate. Stomata aligned more or less parallel to the midrib. Outline of guard cell pairs elliptical, 9-11µm long, 5-6µm wide.

Comments. This species is represented by only two specimens that differ considerably in size and somewhat in shape. As such they could have been derived from different species. They are consistent in leaf shape with several species including *Epacris impressa*. They are smaller and have much smaller and more elongated stomata (~10 x 5 µm *versus* ~22 x 20 µm) than *Epacriphyllum* sp. 7 (below), which has a somewhat similar shape. It also has subsessile leaves compared to the petiolate leaf of *Epacriphyllum* sp. 7.

Epacriphyllum sp. 7 (Fig. 10)

Specimens examined. SCB60_o_Epac1

Description. Leaves hypostomatic, lamina slightly convex above, ovate-lanceolate, tapering more or less uniformly from a point approximately ¼ of the way up the leaf, ~6-7 mm long, ~1.5 mm wide, apparently glabrous, margins thick, entire, apex acute. Petiole straight, 0.5 mm long, 0.6 mm wide. Abaxial epidermal cells elongate, with sinuous walls. Stomata aligned more or less parallel to the midrib. Outline of guard cell pairs almost circular, 20-25µm long, ~20µm wide.

Comments. This species is represented by two specimens that differ considerably in size. It is consistent in leaf shape with several species, including *Epacris impressa*. Comparisons with the only similar fossil species at Stony Creek Basin, *Epacriphyllum* sp. 6, are given above. It also shows some similarity with the Early Oligocene *Epacriphyllum mesibovii* G.J. Jord. & R. S. Hill, although the latter species is widest towards midleaf (Jordan and Hill 1995).

Epacriphyllum sp. 8 (Fig. 11)

Specimens examined. SCB200_o_micro2

Description. Leaves hypostomatic, ovate, widest just below midleaf, ~2.3 mm long, ~1.1 mm wide, slightly convex above, apparently glabrous, margins thick, entire, apex slightly acuminate. Petiole 0.4 mm long, 0.3 mm wide, reflexed at an angle of approximately

90˚. Venation obscure. Abaxial epidermal cells short, 45-70 µm long, 15-25µm wide, with sinuous walls. Stomata aligned more or less parallel to the midrib. Outline of guard cell pairs elliptical, 22-25µm long, 16-18µm wide. Vascular bundles separated from the abaxial mesophyll by several layers of cells.

Comments. This species is represented by only one specimen that shows the characteristic sinuous epidermal cell walls and stomata aligned parallel to these cells of Styphelioideae. The distinctive combination of features is the small, ovate leaves, but large epidermal cells and stomata.

Tribe Cosmelieae

Cosmelieae sp. (Fig. 12)

Specimens examined. SCB190_Spreng; SCB200_Spreng; SCB10_Spreng

Description. Leaves triangular, tapering from a sheathing leaf base, 1.5 – 2.5 mm wide, approximately three times as long as broad, venation parallel with 5-10 veins, very unevenly amphistomatic. Stomata widespread and common on the abaxial surface, sparse on adaxial surface, restricted to the area immediately above the sheathing section. Veins adjacent to the abaxial surface, but with parenchyma or mesophyll cells between the vascular bundles and the adaxial surface. Stomata cyclocytic, outline of guard cell pairs almost circular, 13-15µm long. Epidermal cells aligned parallel with the veins, with very sinuous walls, abaxial cells along veins 40-60µm long, 10-12µm wide, those among the stomata shorter, adaxial cells 30-50µm long, ~10-12µm wide.

Comments. These fossils clearly show the distinctive sheathing leaf bases characteristic of tribes Richeeae and Cosmelieae. They are also amphistomatic, which is almost unknown in Styphelioideae except in these tribes. The stomata and extremely sinuous cell walls are also typical of these tribes. The presence of cyclocytic stomata places this species into Cosmelieae and excludes the Richeeae, which have paracytic stomata (Watson 1967). Also, the vascular bundles are connected by sclerenchyma to both the upper and lower epidermides in almost all species of Richeeae (Watson 1967; G. J. Jordan unpublished data). However, there is one significant difference between this species and extant Cosmelieae. In all species in which the leaf anatomy has been documented (Watson 1967; G. J. Jordan unpublished data), the vascular bundles are in the middle of the mesophyll, or adjacent to the adaxial surface. However, in these fossils the bundles are adjacent to the abaxial leaf surface. Cosmelieae includes *Sprengelia*, which is extant in eastern, mainland Australia, and *Cosmelia* and *Andersonia*, which are endemic to Western Australia. The fossil leaves are consistent in size and shape with several species of *Sprengelia*, e.g. *S. montana* R.Br., *S. monticola* (DC)Druce and small *S. incarnata*. However, given the anomalous placement of the vascular bundles, it is plausible that this represents an extinct genus or species of Cosmelieae.

Tribe Styphelieae

Epacriphyllum sp. 9 (Fig. 13)

Specimens examined. SCB150_o_epac1

Description. Leaves hypostomatic, ovate/oblong, widest just below midleaf, ~3.5 mm long, ~1.8 mm wide, base cordate, flat apart from a downcurved apex, apparently glabrous, margins thick, with scattered trichome bases, apex obtuse. Petiole 0.2mm long, 0.3mm wide, flat, reflexed at an angle of approximately 45˚. Leaf with five main veins running from the petiole, with the central vein straight and the outer veins curved. Abaxial epidermal cells short, 30-40µm long, ~20µm wide, with sinuous walls. Stomata aligned more or less parallel to the midrib. Outline of guard cell pairs broadly elliptical, 18-20µm long, ~16µm wide.

Comments. This species is represented by only one specimen. Features that distinguish it from the other taxa described here are the presence of a blunt, downcurved apex, trichome

bases along the margins, a cordate base and a very short petiole. The presence of only weakly sinuous epidermal cell walls is consistent with Styphelioideae, except *Trochocarpa* (Jordan and Hill 1995). The shape and venation of the leaf is consistent with *Trochocarpa* and *Pentachondra*, although species of *Trochocarpa* lack trichomes along their margins and have strongly sinuous epidermal cell walls (Jordan and Hill 1995). The fossil probably shows most similarity to *Pentachondra* species, which often have ciliate leaf margins, and similar venation, epidermal cells and glabrous leaf surfaces to the fossil (see Jordan and Hill 1995). However, the fossil cannot be confidently assigned to *Pentachondra* due to the absence of particular diagnostic characters.

Epacriphyllum sp. 10 (Fig. 14)

Specimens examined. SCB170_o_epac8 (with anatomy), SCB170_o_epac11, SCB170_o_epac12

Description. Leaves hypostomatic, linear, slightly convex above/narrow-elliptical in cross section, at least 5mm long, 1mm wide, apex acute with a protruding, presumably pungent point, margins thick, entire. Epidermis two cells thick, cells very elongate, 20-25µm wide, up to 150µm long, ~15µm tall with acute ends. Stomata arranged more or less uniformly on each side of the midrib, aligned parallel to the midrib, outline of pair of guard cells elliptical, 24-33µm long, 15-19µm wide. Vascular bundles 50-70µm wide, attached to the abaxial epidermis. Palisade mesophyll 2 layers thick, cells 80µm tall, 25-30µm wide. Spongy mesophyll thin, attached to the abaxial epidermis.

Comments. The sinuous epidermal cell walls typical of Styphelioideae cannot be observed unambiguously in these fossils, but this may be an artefact of preservation. However, the stomatal form and arrangement is typical of the subfamily. Furthermore, the cross-sectional anatomy of these leaves, particularly the location of the small vascular bundle adjacent to the lower epidermis, is characteristic of Styphelioideae. The arrangement of these bundles also suggests parallel or sub-parallel venation.

Epacriphyllum sp. 11 (Fig. 15)**,**

Specimens examined. SCB170_epacris10

Description. Leaves hypostomatic, ovate elliptical, ~ 5 mm long, 1.2 mm wide, concave above, apparently glabrous, margins thick, entire, apex acute, somewhat attenuated into a thick, presumably pungent tip. Abaxial epidermal cells sinuous walled, 15-18µm long, ~10µm wide. Stomata aligned more or less parallel to the epidermal cells. Outline of guard cell pairs elliptical, 15-17µm long, 13-15µm wide. Adaxial epidermal cells very large ~30µm thick. Palisade mesophyll cells in two layers, ~35µm long, ~15µm wide. Vascular bundles adjacent to the abaxial leaf surface.

Comments. This species has all the features of Styphelioideae, and in particular, has the vascular bundles adjacent to the abaxial epidermis, which would suggest that this species belongs to the Styphelieae. It lacks the characteristic trichomes of many Styphelieae, such as *Monotoca* and the *Cyathodes* group of taxa (Figs. 3H-I; see also Quinn *et al*. 2005). The cell walls of the epidermal cells between the stomata are only weakly sinuous, which is also typical of Styphelieae (Jordan and Hill 1995).

Epacriphyllum sp. 12 (Fig. 16)

Specimens examined. SCB200_o_serrate

Description. Leaves hypostomatic, ovate, at least 2.5 mm long (probably approximately 4mm long), ~1mm wide, flat to very slightly convex above, margins flat, finely serrate with acuminate, forward pointing teeth about 30µm long. Venation palmate, but nearly parallel, with approximately 10 main veins. Petiole flat, straight, ~0.3 mm long, ~0.3 mm

wide. Abaxial surface glabrous, stomata restricted to interveinal areas, overall outline of stomata elliptical (14-17µm long, 8-10µm wide), raised to form two banana-shaped ledges, epidermal cells above the veins square ended, sinuous-walled, ~ 50µm long, ~ 8µm wide, epidermal cells between veins weakly sinuous walled, square ended, ~ 20µm long, ~ 15µm wide.

Comments. This species is represented by only one specimen but is distinctive. The serrate margins and venation are very similar to those of *Astroloma humifusum* (Fig. 3B), which differs in having larger leaves and the “teeth" elongated into trichomes. It is possible that such trichomes were present in the living plant that produced the fossils, but were lost in the process of fossilisation.

Epacriphyllum sp. 13 (Fig. 17)

Specimens examined. SCB170styph, SCB170_styph1, SCB170_o_mono1, SCB170_o_mono2, SCB170_o_mono3, SCB170_o_mono4, SCB170_o_mono5, SCB170_o_mono9, SCB170_o_mono15, SCB180_o_mono, SCB180_o_mono2, SCB180_o_mono3, SCB180_o_mono4, SCB200_o_mono, SCB200_o_mono1

Description. Leaves hypostomatic, linear-oblong, sometimes slightly falcate, 4-7 mm long, 0.8-0.9mm wide, flat, margins flat or slightly recurved, finely serrate, apex acute, apex mucronate or pungent. Petiole 0.6-0.7mm long, 0.2-0.3 mm wide, straight or slightly reflexed. Leaf with 3 parallel, main veins, plus two minor veins leading from the base. One to three minor veins leading to the margin at an acute angle from the upper part of the outer main veins. Stomata restricted to interveinal areas, which are slightly depressed and covered with abundant, short conical trichomes. Stomata aligned with veins, elliptical in outline ~25µm long by ~ 18µm wide. Abaxial epidermal cells rectangular, 40-120µm long, 10-15µm wide, walls sinuous, ~8µm tall. Adaxial leaf surface glabrous, epidermal cells elongate, ~ 10-15µm wide, ~ 15µm tall, with strongly sinuous walls. Vascular bundles adjacent to the abaxial leaf surface.

Comments. This is one the most abundant of the species and is consistent with a number of genera, especially *Monotoca*. The characteristic feature is that short, conical trichomes cover the area of the shallow depressions between the veins, and obscure the stomata. The presence of minor veins leading to the margins from the outer main veins is typical of this genus. Some of the leaves are slightly curved to one side, but this is not taken to be sufficient evidence to represent a different species.

Epacriphyllum sp. 14 (Fig. 18)

Specimens examined. SCB170_o_leuc1, SCB140_revolute

Description. Leaves hypostomatic, narrow-oblong, ~3mm long, ~ 0.4mm wide, margins strongly revolute, obscuring most of the lamina. Leaf with one main vein apparent. Petiole ~0.3mm long, ~0.2mm wide, straight. Abaxial lamina with long simple trichomes in the stomatal region. Stomata mostly aligned parallel with the midrib, pair of guard cells elliptical in outline, ~30µm long, ~20µm wide. Adaxial epidermal cells with sinuous walls, 50-70µm long, ~10µm wide, 15-20µm tall. Epidermal cells of the abaxial midrib with sinuous walls very elongated, ~6µm wide.

Comments. This species is clearly consistent with Styphelioideae with sinuous epidermal cell walls. The overall leaf size, leaf form, long trichomes covering the stomatal area and cell sizes (including the unusually tall adaxial epidermal cells) are consistent with *Androstoma verticillata.*

Epacriphyllum sp. 15 (Fig. 19)

*Specimens examined.*SCB170_o_mono6, SCB170_o_mono7, SCB170_o_mono13, SCB170_o_mono14,

Description. Leaves hypostomatic, obovate, 4-5 mm long, 1.1-1.3 mm wide, flat, margins flat in the lower two thirds of the leaf, narrowly revolute in the upper third of the leaf, apex obtuse, shortly mucronate. Leaf with 5-7 subparallel main veins. A few minor veins diverging from the upper part of some of the main veins at an acute angle. Leaf subsessile, petiole straight, ~ 0.3 mm long, ~ 0.5 mm wide. Stomata restricted to interveinal areas, which are slightly depressed and covered with abundant, short conical trichomes. Stomata aligned with veins, elliptical in outline ~18µm long by ~ 14µm wide. Abaxial epidermal cells rectangular, 40-100µm long, 8-10(-15) µm wide, walls weakly sinuous. Adaxial leaf surface glabrous, epidermal cells 50-100µm long, 13-15µm wide with strongly sinuous walls.

Comments. The leaf shape, short conical trichomes and venation make this species consistent with *Monotoca*. It is distinguished from *Epacriphyllum* sp. 13 by the leaf shape (broader, and widest above the middle), the short, broad petiole, the venation (which may be related to the leaf shape) and larger stomata.

Epacriphyllum sp. 16 (Fig. 20)

Specimens examined. SCB170_mono8 (probably), SCB190_epacrid, SCB_360_epacrid

Description. Leaves hypostomatic, elliptical-obovate, 6-7 mm long, 1.6-1.8 mm wide, flat, margins flat, apex acute, mucronate. Leaf with 5-7 subparallel, main veins, plus two minor veins leading from the base. Several minor veins leading to the margin at an acute angle from the upper part of the outer main veins. Petiole 0.5 mm long, 0.3 mm wide, straight. Stomata exposed, restricted to interveinal areas, which are slightly depressed. Stomata aligned with veins, elliptical in outline, 16-18µm long by ~ 12µm wide. Abaxial epidermal cells rectangular, ~60µm long, 8-12µm wide, walls sinuous, but not visibly so on the surface, epidermal cells with a single line of papillae. Adaxial leaf surface glabrous, epidermal cells elongate, ~ 9-15µm wide, with sinuous walls.

Comments. The lack of conical trichomes clearly distinguishes this from *Epacriphyllum* species 13 and 14. This is unlikely to be an artefact – the preservation of anatomy and surface features is so good that it is unlikely that the trichomes have been lost. This species also differs from *Epacriphyllum* species 12, which has toothed/ciliate margins and is smaller (~4 mm vs 6-7 mm).

Epacriphyllum 17 (Fig. 21A-C)

Specimens examined. SCB200_o_styph1

Description. Leaves hypostomatic, narrow-oblong, 4 mm long, ~ 0.4 mm wide, margins recurved. Apex acuminate (presumably pungent). Leaf with 3-5 parallel veins. Petiole ~0.2 mm long, ~0.3 mm wide, flattened, reflexed approximately 45˚. Stomata restricted to interveinal regions, abaxial lamina without conical trichomes in the stomatal region. Stomata aligned parallel with the midrib, pair of guard cells elliptical in outline, ~15µm long, ~10µm wide. Epidermal cells papillose, with strongly revolute walls, ~30µm long, ~7µm wide.

Comments. This species is based on a single specimen. However, the overall leaf form is completely consistent with that of recurved/revolute-margined *Leucopogon* species (e.g. *L. collinus* (Labill.)R.Br.). It differs from *Epacriphyllum* species 14 in having a pungent apex, multiple veins, recurved rather than closely revolute margins, a flattened petiole and much smaller stomata.

Epacriphyllum sp. 18 (Fig 21D-E).

Specimens examined. SCB170_o_mono1

Description. Leaves hypostomatic, narrow elliptical, 2mm long, ~ 0.7mm wide, margins thin, flat. Apex acuminate (presumably pungent). Leaf with 3 parallel veins. Petiole cylindrical ~0.3mm long, ~0.2 mm wide, reflexed to approximately 45˚. Stomata restricted to interveinal regions, abaxial lamina with conical trichomes in the stomatal region. Stomata aligned parallel with the midrib, pair of guard cells elliptical in outline, ~26µm long, ~18µm wide. Epidermal cells with weakly revolute walls, very elongated 40-~100µm long, ~7µm wide.

Comments. This species is based on a single specimen. It has the extremely distinctive conical trichomes typical of the *Cyathodes* group of genera (and some other Styphelioideae). It is a tiny distinctive leaf, broadly consistent with a species such as *Cyathodes dealbata*.

Discussion

The fossils from Stony Creek Basin demonstrate that this place contained high species richness of Styphelioideae at the beginning of the Pleistocene. The diversity included 19 fossil leaf types distinctive enough to suggest that they represented different species (Table 1). These were mostly of the Epacrideae/Archerieae and Styphelieae types, but Cosmelieae were also present. The 170-180cm sample alone contains 13 species. Given the rarity of most species in all the samples, it is plausible that other species of Styphelieae occurred in the source vegetation of this time but are not represented purely through random sampling effects. In particular, an additional six species were present in the other samples from the pit, five of which occurred in the 30 cm below or above the 170-180cm sample.

This species richness is higher than is currently present in the Victorian western uplands. According to Albrecht (1996), only 12 members of Ericaceae (*Acrothamnus hookeri* (Sond.) C.J.Quinn, *Acrotriche prostrata* F. Muell., *A. serrulata* R.Br., *Astroloma humifusum*, *Brachyloma daphnoides* (Sm.)Benth., *Epacris impressa*, *Leucopogon virgatus* (Labill.)R.Br., *L. microphyllus* (Cav.)R.Br., *L. glacialis* Lindl. in T.L. Mitchell, *L. ericoides* (Smith)R.Br., *Lissanthe strigosa* (Smith)R.Br. and *Monotoca scoparia* (Smith)R.Br.) are recorded as now occurring within 10 minutes of latitude or longitude of Stony Creek Basin (an area of more than 1000 km^2). Furthermore, it is exceedingly unlikely that any catchment of comparable size to Stony Creek Basin (0.5 km^2) would contain all of these species. Also, the segregation of fossil morphological forms into species in this paper was relatively conservative – where the variation among forms was small, they were lumped into one taxon. Many closely related modern species differ little in leaf form and some may be indistinguishable (e.g. *Leucopogon exolasius* (F.Muell.)Benth. and *L. ericoides* (Sm.)R.Br.). Thus, it is possible that some of the taxa described here may be equivalent to several modern species. Many of the fossil species are represented by only a few specimens. This suggests that the flora included a large number of uncommon species; as a result other rare species may not have been captured in the fossil assemblage.

Furthermore, the observed diversity at Stony Creek Basin may have underestimated the total diversity in the catchment. In support of this, the taphonomic analysis of Lake Dobson in central Tasmania by Hill and Gibson (1986) showed a significant under-representation of local diversity. That study sampled leaves in superficial sediments. The leaves therefore represented the contribution from modern vegetation to sediments, and were comparable to fossil assemblages. Lake Dobson represents a catchment of similar size (~0.8 km^2) to that of Stony Creek Basin, but is within one of the centres of diversity of Styphelioideae. In spite of intensive sampling, (156 sediment samples containing over 27,000 identified leaves), Hill and Gibson (1986) could only recognise 6 distinct leaf types of Styphelioideae from the sediments. Thus, the true species richness of Styphelioideae of the

Lake Dobson catchment (20 species; Table 2) was over three times that indicated from the sediment samples.

It is therefore plausible that the local species richness in and around Stony Creek Basin was similar to, or even greater than, that found in modern floras in the centres of diversity of the group. However, neither the tribal nor the generic diversity was very high. The fossil assemblage contains three of the tribes of Styphelioideae (Epacrideae, Cosmelieae and Styphelieae), whereas the generic diversity is difficult to determine – the minimum value is three (the subfamilies), but six or seven is probably a more realistic estimate (assuming that the fossil species resembling *Monotoca*, *Leucopogon*, *Androstoma*, *Pentachondra* and *Astroloma* were derived from taxa equivalent to separate modern genera).

Members of Styphelieae and *Epacris*-like species (most, if not all, probably members of Epacrideae) dominate the fossil flora. The Epacrideae are best represented in New South Wales and Tasmania, with approximately 25 species in each region (Powell 1992; Buchanan 2005). The high diversity of *Epacris*-like species is consistent with a relatively wet climate (as found in much of Tasmania and central eastern New South Wales). The Styphelieae are diverse in each of the centres of diversity of the subfamily, particularly in Western Australia. There is no indication of the presence of the highly phylogenetically isolated groups found in western Tasmania (*Archeria*, *Prionotes* and Richeeae), although it remains possible that some of the *Epacris*-like taxa could be *Archeria* or some other near-basal lineage that is now extinct. Thus, the diversity of Styphelioideae found in the Stony Creek Basin flora appears to be mainly in the groups that now make up large parts of the radiation of this subfamily, especially in eastern Australia.

The presence of such high diversity outside the present centres of diversity of the subfamily can be explained in two ways. The diversity in the modern centres of diversity may have immigrated from elsewhere (e.g. Victoria's western uplands). However, this appears unlikely considering the very high levels of endemism of the centres of diversity, including endemic genera (e.g. Hill and Orchard 1999; Powell 1992) and the strong association of these centres of diversity with extremely low nutrient soils (which are much less well represented in Victoria's western uplands). Alternatively, the geographic range of diverse epacrid floras may have been much wider than it now is, but local extinction reduced the diversity of some regions (e.g. the Victorian western uplands). Since there is now clear evidence for extensive Pleistocene extinctions in southern Australia (e.g. Jordan 1997; Sniderman *et al.* 2007), the latter is the most plausible explanation for the Stony Creek Basin data. This would then imply that the modern radiation of Styphelioideae in eastern Australia was well advanced by the beginning of the Pleistocene, at a time when warm temperate rainforest still occurred in the Central Highlands of Victoria (Sniderman et al. 2007), a region now dominated by cool temperate sclerophyllous vegetation and entirely lacking rainforest.

Acknowledgments

We thank Nick Porch for help with excavating the pit at Stony Creek Basin and extracting specimens from the core material. We thank Chris Quinn, John Conran and an anonymous reviewer for comments on the manuscript. We also thank the Central Science Laboratory, University of Tasmania, and the Centre for Nanoscale Systems, Harvard University for use of, and assistance with, scanning electron microscopes. Funding for excavations at Stony Creek Basin was supplied by Peter Kershaw, Monash University.

Literature Cited

Albrecht DE 1996 Epacridaceae. Pages 464-509 *in* NG Walsh, TJ Entwistle, eds. Flora of Victoria. Vol. 4, Inkata Press, Melbourne, Australia.

Buchanan AM 2005 A census of the vascular plants of Tasmania and index to The Student's

Flora of Tasmania. Tasmanian Herbarium Occasional Publication 7.
Carpenter RJ 1991 Palaeovegetation and Environment at Cethana, Tasmania. PhD diss. University of Tasmania, Hobart, Australia.
Carpenter RJ, Jordan GJ, Hill RS 1994 *Banksieaephyllum taylorii* (Proteaceae) from the Late Paleocene of New South Wales and its relevance to the origin of Australia's scleromorphic flora. Aust Syst Bot 7: 385-392.
Cherry W, Gadek PA, Brown EA, Heslewood MM, Quinn CJ 2001 *Pentachondra dehiscens* sp. nov. - an aberrant new member of Styphelieae. *Aust Syst Bot* **14**: 513–533.
Cranfield RJ 1998 *Brachyloma nguba* (Epacridaceae), a new species from the south-west of Western Australia. Nuytsia 12: 179–183.
Cranfield RJ 2002 *Conostephium magnum* (Epacridaceae), a new species from Western Australia. *Nuytsia 15: 21–25.*
Crayn DM, Kron KA, Gadek PA, Quinn CJ 1998 Phylogenetics and evolution of epacrids: a molecular analysis using the plastid gene *rbc*L with a reappraisal of the position of *Lebetanthus. Aust J Bot 46: 187-200.*
Crayn DM, Brown EA, Powell JM 2003 A revision of *Lissanthe* (Styphelioideae: Ericaceae). Aust Syst Bot 16: 595–619.
Crayn DM, Hislop M, Heslewood MM 2005 Additions to *Lissanthe* (Styphelioideae: Ericaceae) in Western Australia: *L. synandra* sp. nov. and *L. pleurandroides* comb. nov. Aust Syst Bot 18: 1-7.
Crisp M, Cook L, Steane DA 2004 Radiation of the Australian flora: what can comparisons of molecular phylogenies across multiple taxa tell us about the evolution of diversity in present-day communities? Phil. Trans. R. Soc. Lond. B 359: 1551–1571
de Lange PJ, Sawyer JWD, Rolfe JR 2006 New Zealand Indigenous Vascular Plant Checklist. New Zealand Plant Conservation Network, Wellington, New Zealand. 94 pp.
Dettmann ME 1994 Cretaceous vegetation: the microfossil record. Pages 143-170 *in* RS Hill, ed. History of the Australian Vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge.
Frakes LA 1999 Evolution of Australian environments. Flora of Australia 1 (2nd edn) 163-203.
Gradstein, FM, Ogg, JG, Smith, AG 2004 A Geological Time Scale 2004. Cambridge University Press, Cambridge.
Hill RS 1994 The history of selected Australian taxa. Pages 390-420 *in* RS Hill, ed. History of the Australian Vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge.
Hill RS 1998 Fossil evidence for the onset of xeromorphy and scleromorphy in Australian Proteaceae. Aust Syst Bot 11: 391–400
Hill RS, Gibson N 1986 Distribution of potential macrofossils in Lake Dobson, Tasmania. J Ecol 7**4**: 373-84.
Hill RS, Orchard AE 1999 Composition and endemism of vascular plants. Pages 89-124 *in* JB Reid, RS Hill, MJ Brown, MJ Hovenden, eds. Vegetation of Tasmania. Australian Biological Resource Study, Melbourne, Australia.
Hopper SD, Gioia P 2004 The Southwest Australian floristic region: evolution and conservation of a global hot spot of biodiversity. Ann Rev Ecol Evol Syst 35: 623–650.
Jackson WD 1999 The Tasmanian environment. Pages 1-10 *in* JB Reid, RS Hill, MJ Brown, MJ Hovenden, eds. Vegetation of Tasmania. Australian Biological Resource Study, Melbourne, Australia.
Jordan GJ 1997 Evidence of Pleistocene plant extinction and diversity from Regatta Point, western Tasmania, Australia. Bot J Linn Soc 12**3**: 45-71.
Jordan GJ 2001 An investigation of long-distance dispersal based on species native to both Tasmania and New Zealand. Aust J Bot 49: 333-340.

Jordan GJ, Carpenter RJ, Hill RS 1998 Macrofossil evidence of past diversity of Proteaceae in Tasmania, including nine new species. Aust Syst Bot 11: 465-501.
Jordan GJ, Hill RS 1995 Oligocene leaves of Epacridaceae from Little Rapid River, Tasmania and the identification of fossil Epacridaceae leaves. Aust Syst Bot 8: 71-83.
Jordan GJ, Hill RS 1996 The fossil record of the Epacridaceae. Ann Bot 77: 341-346.
Keighery GJ 1996. Phytogeography, biology and conservation of Western Australian Epacridaceae. Ann Bot 77: 347-356.
Keighery GJ 2002 A new species of *Conostephium* (Epacridaceae) from gypsum dunes in Western Australia. Nordic J Bot 22: 49–52.
Klak C, Reeves G, Hedderson T 2004. Unmatched tempo of evolution in Southern African semi-desert ice plants. Nature 427: 63-65.
Kron KA, Judd WS, Stevens PF, Crayn DM, Anderberg AA, Gadek PA, Quinn CJ, Luteyn JL 2002 Phylogenetic classification of Ericaceae: Molecular and morphological evidence. Bot Rev 68: 335–423.
Lisiecki LE, Raymo ME 2005 A Pliocene-Pleistocene stack of 57 globally distributed benthic ∂^{18}O records. Paleoceanography 20: 1-17.
Powell JM 1992 Epacridaceae. Pages 401-434 *in* GJ Harden, ed. Flora of NSW. University of NSW Press, Sydney, Australia
Quinn CJ, Brown EA, Heslewood MM, Crayn DM 2005 Generic concepts in Styphelieae (Ericaceae): the *Cyathodes* group. Aust Syst Bot 18: 439-454.
Scriven LJ, Hill RS 1995 Macrofossil Casuarinaceae: their identification, including the oldest macrofossil record, *Gymnostoma antiquium* sp. nov. from the Late Paleocene of New South Wales, Australia. Aust Syst Bot 8: 1035-1053.
Sniderman JMK, Pillans B, O'Suillivan PB, Kershaw AP 2007 Climate and vegetation in southeastern Australia respond to southern hemisphere insolation forcing in the Late Pliocene-Early Pleistocene. Geology 35**:**41-44.
Stevens PF, Luteyn J, Oliver EGH, Bell TL, Brown EA, Crowden RK, George AS, Jordan GJ, Ladd P, Lemson K, McLean CB, Menadue Y, Pate JS, Stace HM, Weiller CM 2004. Ericaceae. Pages 145-194 *in* K Kubitzki, ed. The Families and Genera of Vascular Plants. Vol. 6. Springer-Verlag, Berlin..
Taaffe G, Brown EA, Crayn DM, Gadek PA, Quinn CJ 2001 Generic concepts in Styphelieae: resolving the limits of *Leucopogon*. Aust J Bot 49: 107–120.
Watson L 1967 Taxonomic implications of a comparative anatomical study of Epacridaceae. New Phyt 66: 495-504.
Weiller CM 1999 *Leptecophylla*, a new genus for species formerly included in *Cyathodes* (Epacridaceae). Muelleria 12: 195–214.

Table 1. Summary of fossil Styphelioideae in different samples from Stony Creek Basin. Comparable extant species are also listed. These are species similar to, but not necessarily closely related to the fossils

Species	**comparable taxa**	**samples**
Tribe Epacrideae or Archerieae		
Epacriphyllum sp. 1	tiny *Epacris* (e.g. *E. microphylla*)	170, 190
Epacriphyllum sp. 2	*Epacris* spp. (e.g. *E. obtusifolia* Smith)	170
Epacriphyllum sp. 3	*Epacris* spp. (e.g. *E. obtusifolia*)	90, 1985
Epacriphyllum sp. 4	*Epacris* spp. (e.g. *E. heteronema*)	170
Epacriphyllum sp. 5	*Epacris* spp.	150, 170, 180, 190, 200, 1985
Epacriphyllum sp. 6	*Epacris* spp.	180, 200
Epacriphyllum sp. 7	*Epacris* spp. (e.g. *E. impressa*)	60
Epacriphyllum sp. 8	*Epacris* spp.	170, 200, 150
Tribe Cosmelieae		
Cosmelieae sp.	*Sprengelia* spp.	10, 170, 190
Tribe Styphelieae		
Epacriphyllum sp. 9	*Pentachondra* spp.	150
Epacriphyllum sp. 10	*Leucopogon* spp.	170
Epacriphyllum sp. 11	*Leucopogon* spp.	170
Epacriphyllum sp. 12	*Astroloma humifusum*	200
Epacriphyllum sp. 13	*Monotoca* spp.	170, 180, 200
Epacriphyllum sp. 14	*Androstoma verticillata*	140, 170
Epacriphyllum sp. 15	*Monotoca* spp.	170
Epacriphyllum sp. 16	*Leucopogon* spp.	170, 190, 360
Epacriphyllum sp. 17	*Leucopogon* spp. (e.g. *L. collinus*)	200
Epacriphyllum sp. 18	*Cyathodes dealbata*	170

Table 2. Species of Styphelioideae currently present in the Lake Dobson catchment

Archeria serpyllifolia Hook.f.	*Cyathodes dealbata*
C. straminea R.Br.	*C. glauca* Labill.
Dracophyllum minimum F. Muell.	*Epacris serpyllifolia* R.Br.
Leptecophylla juniperina	*Acrothamnus montanus* (R.BR.) C.J. Quinn
Monotoca empetrifolia R.Br.	*Planocarpa petiolaris* (DC)Weiller
Pentachondra pumila (Forst. & G.Forst.) R.Br.	*Richea Xcurtisiae* A.M. Gray
R. pandanifolia Hook.f.	*R. scoparia* Hook.f.
R. sprengelioides (R.Br.)F.Muell.	*R. gunnii* Hook.f.
Sprengelia incarnata	*S. montana*
Trochocarpa cunninghamii	*T. thymifolia* (R.Br.)Sprengel

FIGURES

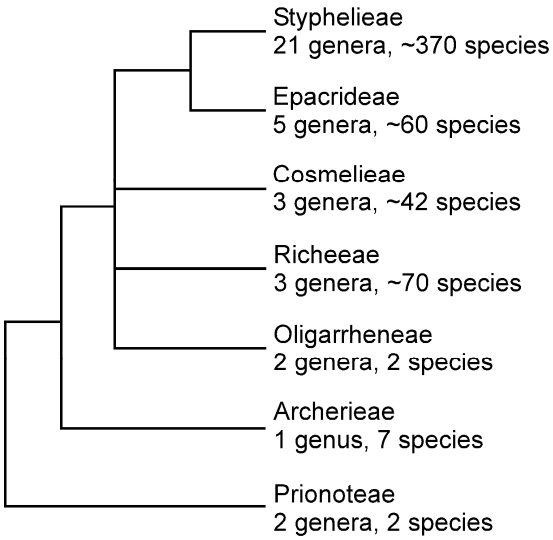

Fig. 1 Species richness and phylogeny of tribes of Styphelioideae. The phylogeny follows Crayn *et al*. 2000. Tribal classification follows Crayn et al. (1998). The species richness in each group follows Stevens et al. (2004) and Quinn et al. (2005).

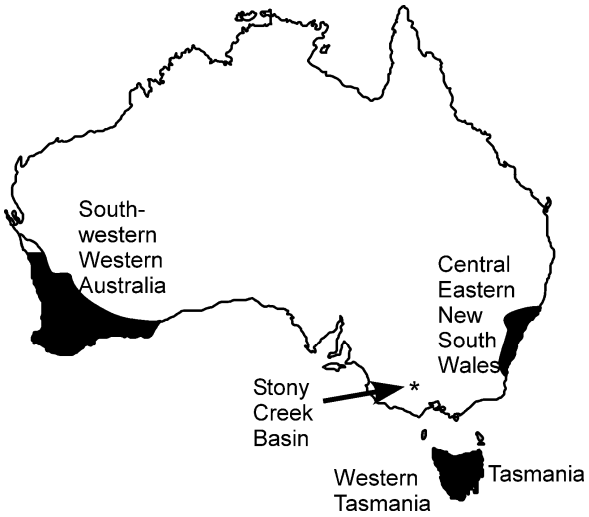

Fig. 2 Map of Australia showing the fossil site and the main centres of diversity of Styphelioideae (which contain over 75% of the species of the subfamily).

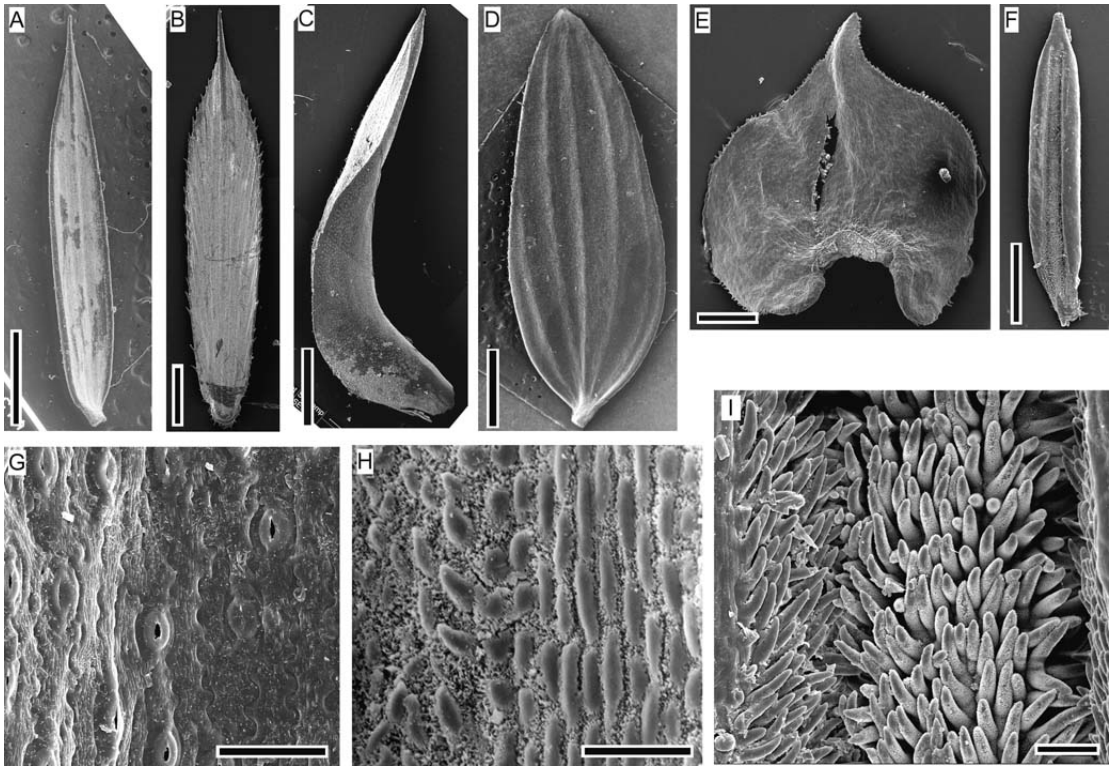

Fig. 3 Scanning electron micrographs of extant species of Styphelioideae.
A. Abaxial leaf surface of *Leptecophylla juniperina* (bar=2 mm).
B. Lateral view of a leaf of *Astroloma humifusum* (Benth.) R.Br. (bar=1 mm).
C. Abaxial leaf surface of *Sprengelia incarnata* (bar=2 mm).
D. Abaxial leaf surface of *Trochocarpa cunninghamii* (DC.) W.M.Curtis (bar=2 mm).
E. Abaxial leaf surface of *Epacris microphylla* R.Br. (bar=0.5 mm).
F. Abaxial leaf surface of *Androstoma verticillata* (Hook.f.) C.J.Quinn (bar=0.5 mm).
G. Abaxial leaf surface of *Epacris impressa* Labill. showing stomata and epidermal cells aligned with each other, and the outlines of the sinuous epidermal cell walls (bar = 50μm).
H. Abaxial leaf surface of *Leptecophylla juniperina* showing the short conical trichomes covering the stomatal regions (left) and elongated cells over the vein (right) (bar=50 μm).
I. Abaxial leaf surface of *Androstoma verticillata* showing elongated conical trichomes in the groove between a recurved margin and the midrib (bar=50 μm).

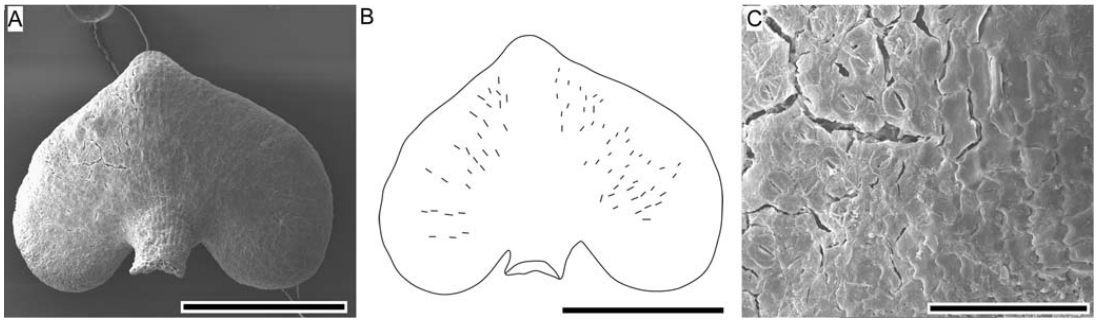

Fig. 4 Scanning electron micrographs and one line drawing of fossil leaves of *Epacriphyllum* species 1 (SCB190_o_epac1) from Stony Creek Basin.
A. Abaxial leaf surface (bar=500μm).
B. Line drawing of abaxial leaf surface showing position and alignment of stomata (bar=500μm).
C. Detail of abaxial leaf surface showing stomata, and shape of epidermal cells (bar=100μm).

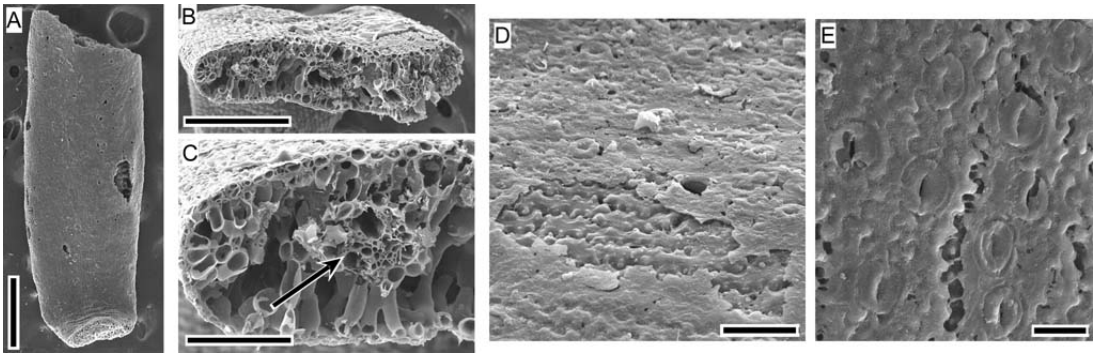

Fig. 5 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 2 (SCB170_o_epac9) from Stony Creek Basin.
A. Abaxial surface (bar = 500µm).
B. Cross section (bar= 300µm).
C. Cross section (bar= 100µm) showing vascular bundle placed approximately midway between adaxial and abaxial surfaces (arrow).
D. Abaxial leaf surface showing stomata and elongate epidermal cells with sinuous walls (bar= 50µm).
E. Abaxial leaf surface showing stomata and sinuous cell walls (bar= 20µm).

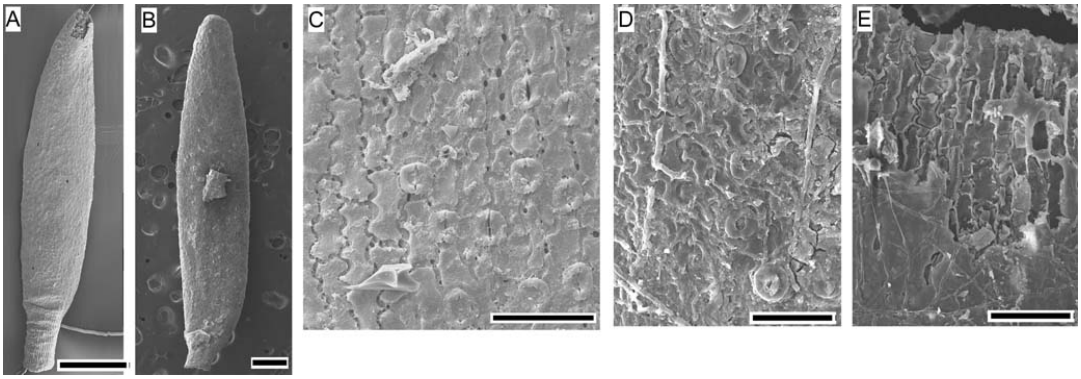

Fig. 6 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 3 from Stony Creek Basin.
A. Abaxial leaf surface of SCB90_o_epac3 (bar=500µm).
B. Abaxial leaf surface of SCB1985_epac2 (bar=500µm).
C. Abaxial leaf surface of SCB90_o_epac3 showing stomata and relatively short epidermal cells with sinuous walls (bar=50µm).
D. Abaxial leaf surface of SCB1985_epac2 showing stomata and epidermal cells (bar=50µm).
E. Adaxial leaf surface of SCB1985_epac2 showing elongate epidermal cells with sinuous walls (bar=100µm).

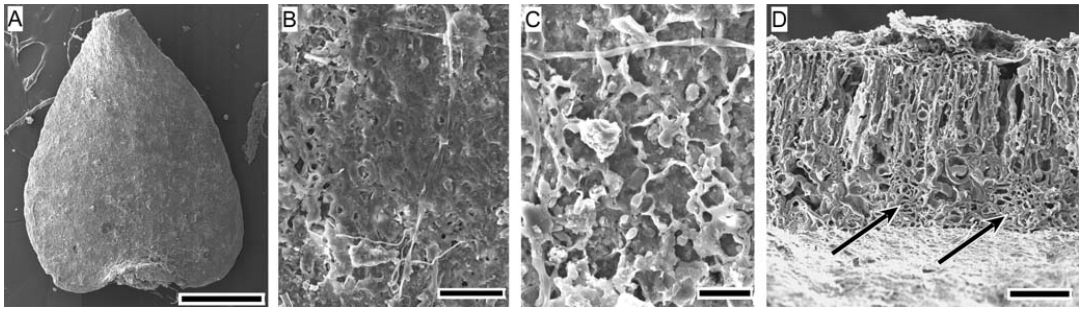

Fig. 7 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 4 (SCB170_epacris1) from Stony Creek Basin.
A. Abaxial leaf surface (bar=1mm).
B. Detail of abaxial leaf surface showing stomata, and shape of epidermal cells (bar=50µm).
C. Detail of eroded abaxial leaf surface showing the sinuous cell walls of the epidermal cells of veinal region (bar=20µm).
D. Cross section of lamina. Note that there has been artefactual thickening of the cell walls of some tissues.

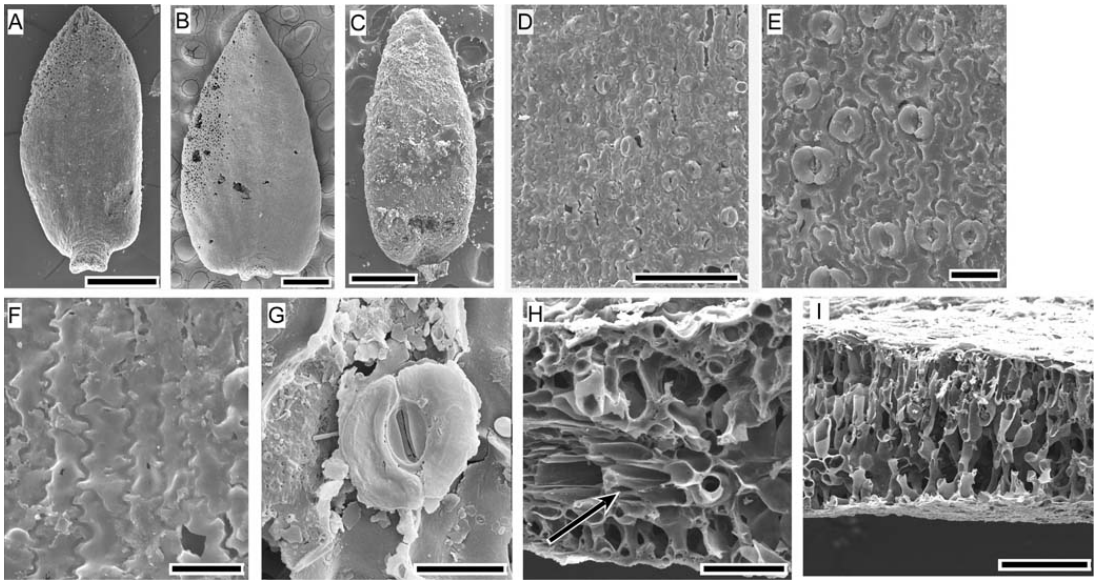

Fig. 8 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 5 from Stony Creek Basin.
A. Abaxial leaf surface of SCB190_epac2 (bar=500µm).
B. Abaxial leaf surface of SCB180_epac3 (bar=500µm).
C. Adaxial leaf surface of SCB1985_epac (bar=500µm).
D. Partially eroded abaxial leaf surface of SCB190_epac2 showing stomata and epidermal cells (bar=100µm).
E. Partially eroded abaxial leaf surface of SCB1985_epac showing stomata and short epidermal cells with sinuous walls (bar=20µm).
F. Adaxial leaf surface of SCB190_epac2 showing short epidermal cells with sinuous walls (bar=20µm).
G. Eroded adaxial leaf surface of SCB190_epac2 showing a stoma (bar=10µm).
H. Cross section of SCB190_epac2 showing a vascular bundle (arrow) with mesophyll tissue above and below it. Note also the small epidermal cells (bar=50µm).
I. Cross section of SCB190_epac2 showing mesophyll tissue (bar=100µm).

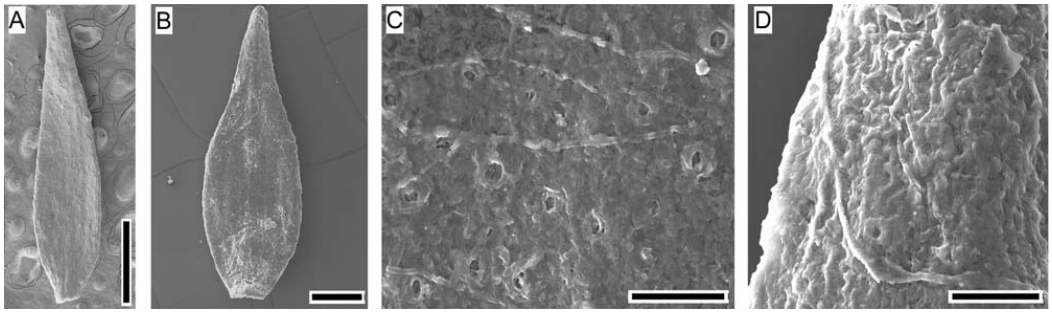

Fig. 9 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 6 from Stony Creek Basin.
A. Abaxial leaf surface of SCB180_o_epac4 (bar = 1mm).
B. Abaxial leaf surface of SCB200_o_tiny_epac (bar = 0.5 mm).
C. Abaxial leaf surface of SCB200_o_tiny_epac showing stomata (bar = 50µm).
D. Abaxial leaf surface of SCB200_o_tiny_epac showing collapsed surface indicating the presence of sinuous epidermal cell walls (bar = 50µm).

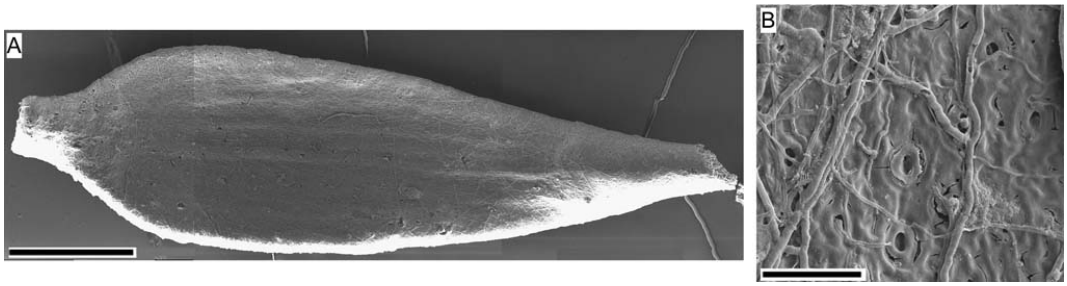

Fig. 10 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 7 (SCB60_o_Epac1) from Stony Creek Basin.
A. Abaxial leaf surface (bar = 1mm).
B. Abaxial leaf surface of showing stomata aligned with the midrib and indications of the presence of sinuous cell walls (bar = 50µm).

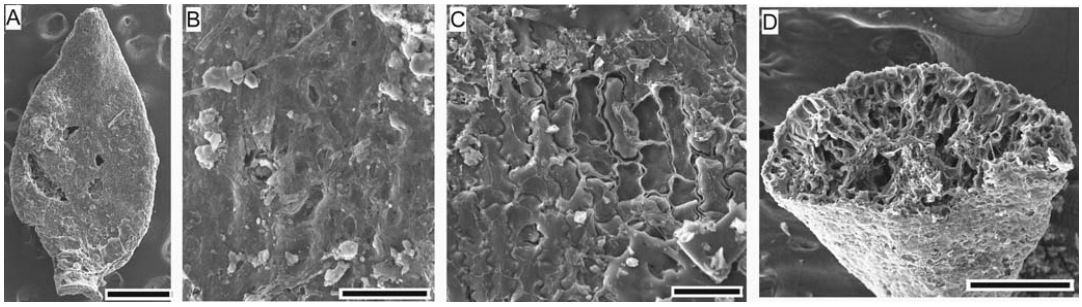

Fig. 11 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 8 from Stony Creek Basin.
A. Abaxial surface of SCB200_o_micro2 (bar = 500µm).
B. Abaxial surface of SCB200_o_micro2 showing stomata (bar = 50µm).
C. Partially eroded adaxial surface of SCB200_o_micro2 showing short, sinuous-walled epidermal cells (bar = 50µm).
D. Cross section of SCB200_o_micro2 showing distribution of mesophyll cells and vascular bundles (bar = 200µm).

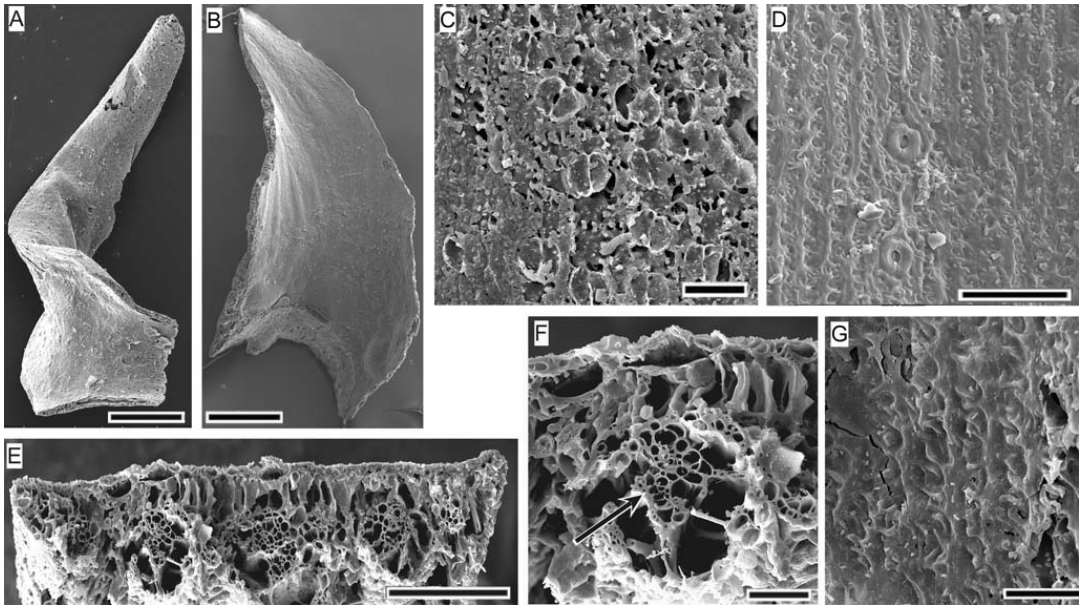

Fig. 12 Scanning electron micrographs of fossil leaves of Cosmelieae sp. from Stony Creek Basin.
A. Abaxial surface of SCB200_Spreng (bar = 500µm). The lateral parts of the leaf base have been broken off.
B. Composite micrograph of abaxial surface of SCB190_Spreng (bar = 500µm).
C. Partially eroded abaxial surface of SCB190_Spreng showing stomata and sinuous cell walls (bar = 50µm).
D. Abaxial surface of SCB200_Spreng showing cyclocytic stomata and sinuous-walled epidermal cells (bar = 50µm).
E. Cross section of SCB200_Spreng showing several vascular bundles adjacent to the adaxial surface (bar = 100µm).
F. Cross section of SCB200_Spreng showing a vascular bundle adjacent to the adaxial surface and separated from the abaxial surface by mesophyll cells (arrow) (bar = 20µm).
G. Adaxial surface of SCB10_Spreng showing depressions indicating sinuous walled epidermal cells (bar = 20µm).

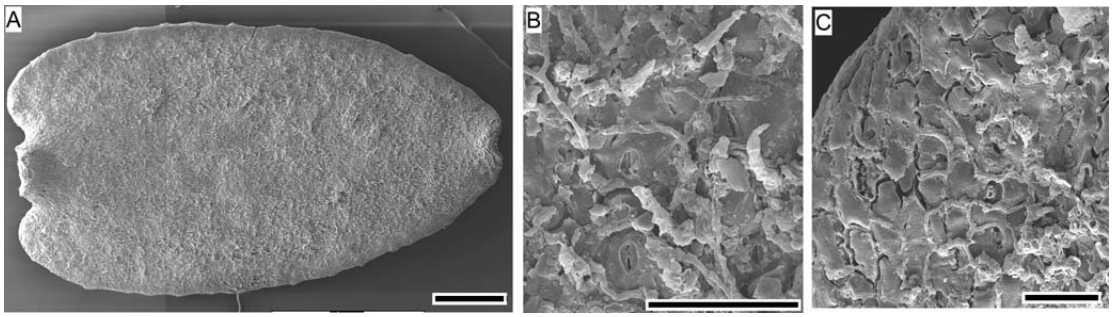

Fig. 13 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 9 (SCB150_o_Epac1) from Stony Creek Basin.
A. Abaxial surface (bar = 500µm).
B. Abaxial surface showing stomata (bar = 50µm). The specimen shows some fungal overgrowth (the wavy hair-like structures).
C. Partially eroded abaxial surface showing sinuous-walled epidermal cells (bar = 50µm).

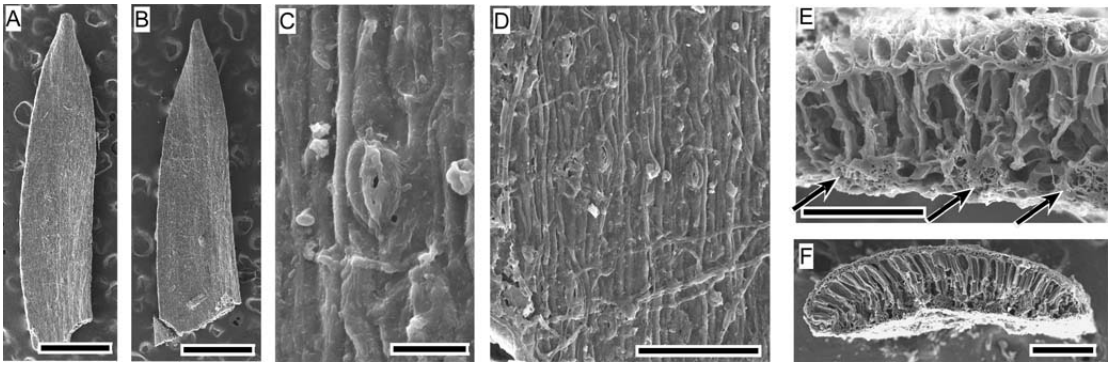

Fig. 14 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 10 from Stony Creek Basin.
A. Abaxial surface of SCB170_o_epac12 (bar = 1mm).
B. Abaxial surface of SCB170_o_epac11 (bar = 1mm).
C. Detail of abaxial surface of SCB170_o_epac8 showing a stoma (bar= 20µm).
D. Detail of abaxial surface of SCB170_o_epac8 showing stomatal distribution (bar= 100µm).
E. Cross section of SCB170_o_epac12 showing vascular bundles attached to the lower epidermis (bar= 100µm).
F. Cross section of SCB170_o_epac8 (bar= 200µm).

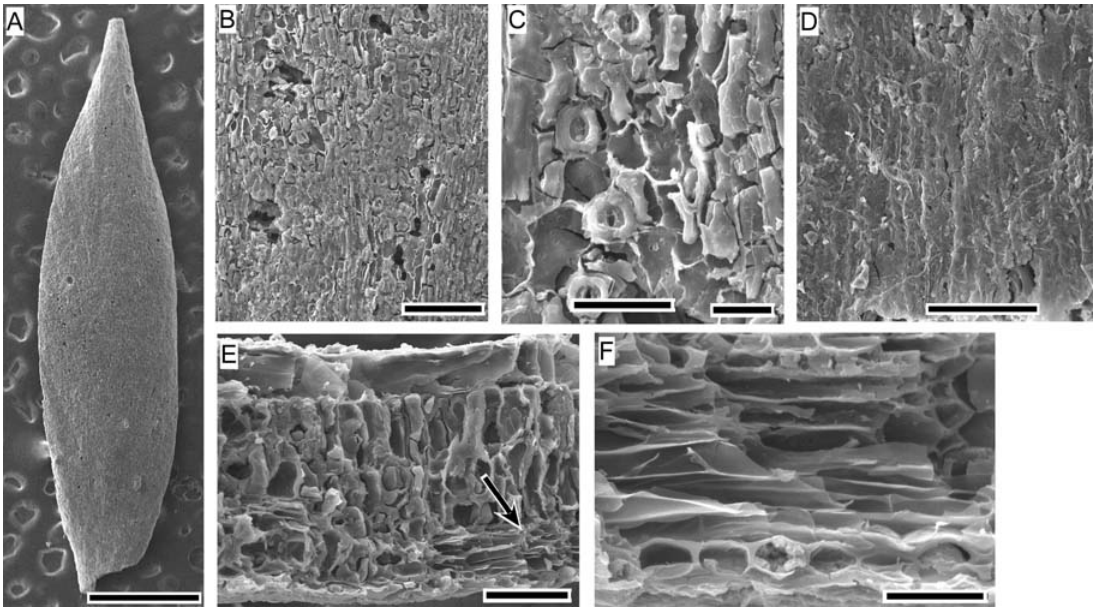

Fig. 15 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 11 (SCB170_o_Epac10) from Stony Creek Basin.
A. Abaxial surface (bar = 1mm).
B. Partially eroded abaxial surface showing stomatal distribution (bar = 100µm).
C. Partially eroded abaxial surface showing stomata and weakly sinuous-walled epidermal cells (bar = 20µm).
D. Adaxial surface showing sinuous-walled epidermal cells (bar = 100µm).
E. Cross section showing tall adaxial epidermal cells. Note also vascular bundle adjacent to the abaxial epidermis (arrow) (bar = 50µm).
F. Cross section showing vascular bundle adjacent to the abaxial epidermis (bar = 20µm).

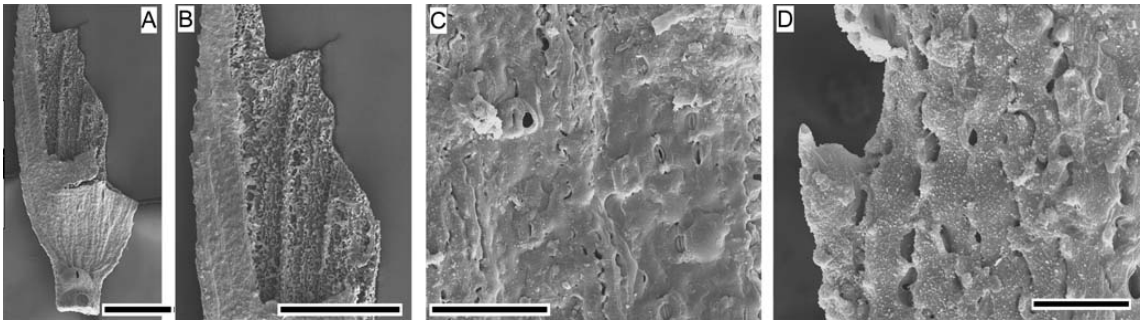

Fig. 16 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 12 (SCB200_o_serrate) from Stony Creek Basin.
A. Abaxial surface (bar = 0.5mm).
B. Abaxial surface showing teeth, veins and stomatal distribution (bar = 0.5mm).
C. Abaxial surface showing stomata and sinuous cell walls (bar = 50µm).
D. Margin of abaxial surface showing a tooth/trichome base (bar = 20µm).

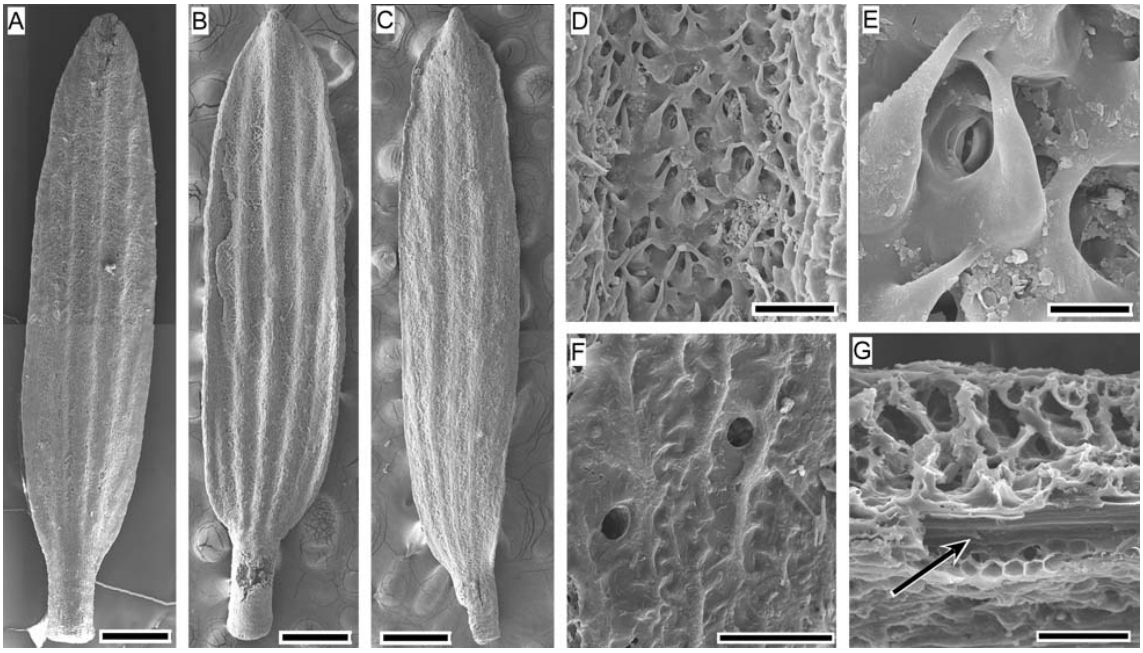

Fig. 17 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 13 from Stony Creek Basin.
A. Abaxial surface of SCB200_Mono1 (bar = 0.5mm).
B. Abaxial surface of SCB180_Monotoca_like (bar = 0.5mm).
C. Abaxial surface of SCB180_Mono_o_4 (bar = 0.5mm).
D. Abaxial surface of SCB180_Mono_o_3 showing stomata and trichomes restricted to interveinal regions, and sinuous epidermal cell walls of veinal regions (bar = 50µm).
E. Abaxial surface of SCB180_Mono_o_3 showing a stoma and trichomes (bar = 10µm).
F. Adaxial surface of SCB200_Mono_o_1 showing sinuous epidermal cell walls (bar = 20µm).
G. Cross section of SCB170_Mono_o_4 showing a vascular bundle adjacent to the small epidermal cells of the abaxial surface (bar = 50µm).

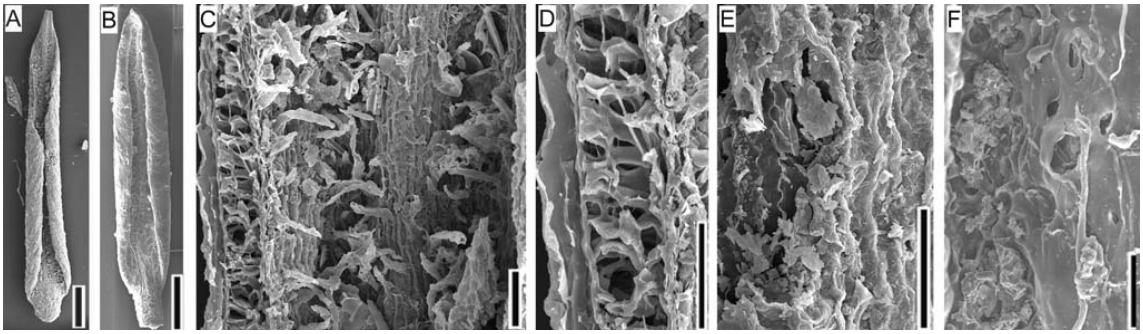

Fig. 18 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 14 from Stony Creek Basin.
A. Abaxial surface of SCB140_o_revolute (bar = 0.5mm).
B. Abaxial surface of SCB170_o_leuc1 (bar = 0.5mm).
C. Upper part of abaxial surface of SCB140_o_revolute showing the revolute margin, midrib and long trichomes (bar = 50μm).
D. Longitudinal section of SCB140_o_revolute showing the tall epidermal cells and tall mesophyll (bar = 50μm).
E. Partially eroded region of adaxial surface of SCB140_o_revolute showing the elongate epidermal cells with sinuous walls (bar = 50μm).
F. Upper part of abaxial surface of SCB170_o_leuc1 showing stomata (bar = 50μm).

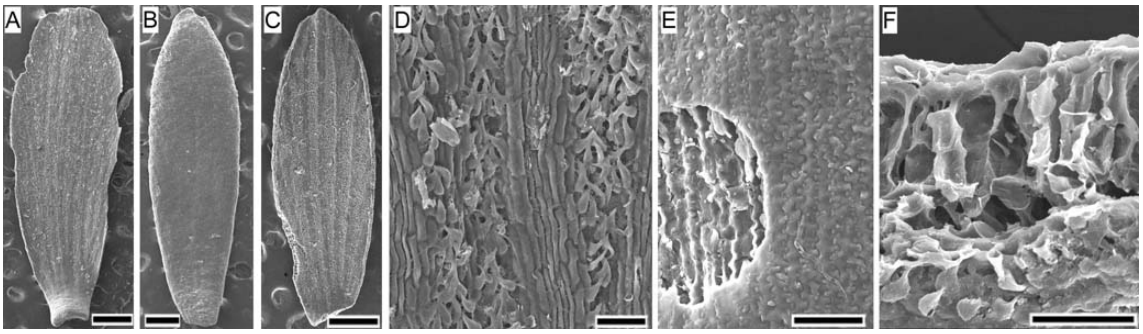

Fig. 19 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 15 from Stony Creek Basin.
A. Abaxial surface of SCB170_o_Mono7 (bar = 0.5mm).
B. Adaxial surface of SCB170_o_Mono14 (bar = 0.5mm).
C. Abaxial surface of SCB170_o_Mono6 (bar = 0.5mm).
D. Abaxial surface of SCB170_o_Mono6 showing stomata and trichomes restricted to interveinal regions, and sinuous epidermal cell walls of veinal regions (bar = 50μm).
E. Adaxial surface of SCB170_o_Mono14 showing sinuous epidermal cell walls. Part of the surface has been eroded (bar = 50μm).
F. Cross section of SCB170_o_Mono14 showing epidermal and mesophyll cells (bar = 50μm).

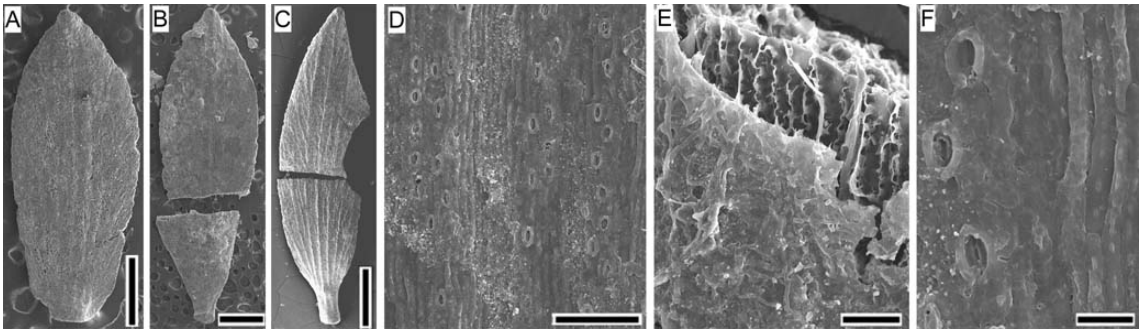

Fig. 20 Scanning electron micrographs of fossil leaves of *Epacriphyllum* species 16 from Stony Creek Basin.
A. Abaxial surface of SCB170_o_Mono8 (bar = 1mm).
B. Abaxial surface of SCB360_epacrid (bar = 1mm).
C. Abaxial surface of SCB190_o_Epacrid (bar = 1mm).
D. Abaxial surface of SCB360_epacrid showing stomata restricted to interveinal regions, and sinuous epidermal cell walls of veinal regions (bar = 100μm).
E. Partially eroded adaxial surface of SCB360_epacrid showing sinuous epidermal cell walls (bar = 50μm).
F. Abaxial surface of SCB360_epacrid showing small papillae on interveinal region (bar = 20μm).

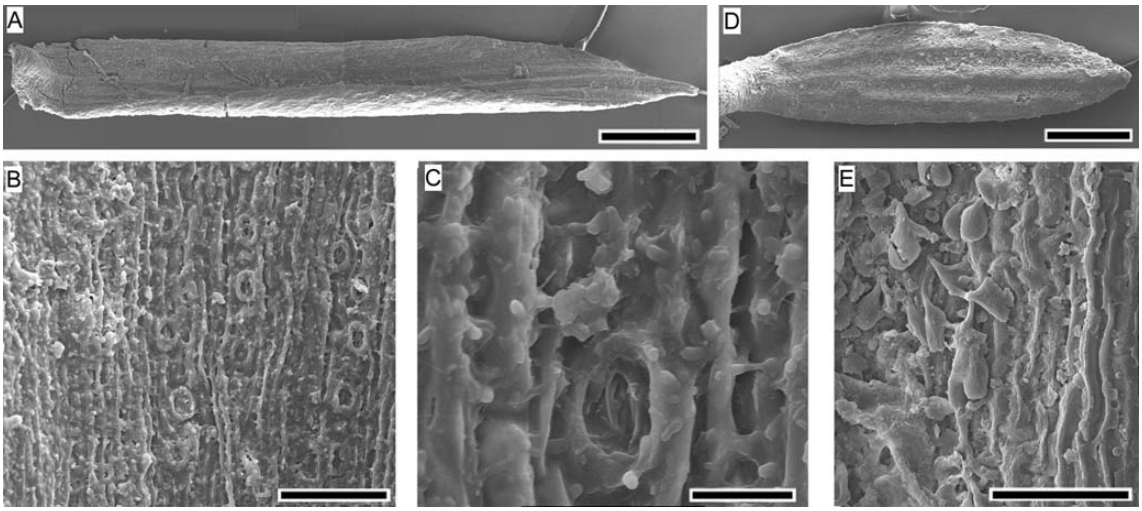

Fig. 21 Scanning electron micrographs of fossil leaves of species 17 (SCB200_o_Styph1) and 18 (SCB170_o_mono1) from Stony Creek Basin.
A. Abaxial surface of SCB200_o_Styph1 (bar = 0.5mm).
B. Abaxial surface of SCB200_o_Styph1 showing aligned stomata restricted to interveinal regions, and sinuous epidermal cell walls of veinal regions (bar = 50μm).
C. Abaxial surface of SCB200_o_Styph1 showing a stoma and degraded waxes (bar = 10μm).
D. Abaxial surface of SCB170_o_mono12 (bar = 0.5mm).
E. Abaxial surface of SCB170_o_mono12 showing outlines of sinuous-walled epidermal cells, stomata aligned parallel to the midrib and obscured by conical trichomes (bar = 50μm).